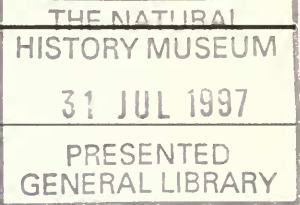


Notes on the diatom species *Tetracyclus castellum* (Ehrenb.) Grunow with a description of *Tetracyclus pseudocastellum* nov. sp.

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SYNOPSIS. This paper reviews the evidence for retaining the taxon described by Ehrenberg as *Bibliarium castellum* Ehrenb. (transferred to the genus *Tetracyclus* by Grunow). Consideration of numerous new names proposed since Ehrenberg establishes that *T. castellum* is a valid taxon which has been re-described several times during the period 1903-1983. While previously considered to be known only from a few fossil specimens, this paper establishes that it has been recorded as living (from Iceland). In addition, a better understanding of *T. castellum* has revealed a new fossil species from China, *T. pseudocastellum*.

INTRODUCTION

The diatom genus *Tetracyclus* Ehrenb. (Bacillariophyta) comprises at least 30 species, of which only five have been reported living, the remainder occurring exclusively as fossils (Williams, 1987, 1989, 1996). The taxonomy of the genus has more or less relied on the shape and dimensions of the valve as well as the frequency of particular valve characters, such as striae and ribs (Hustedt, 1914; Li, 1982a, b, 1984). While the majority of species are either elliptical or circular in valve outline, there are a few taxa that have more or less star-shaped valves. Two of these species, *T. emarginatus* (Ehrenb.) W. Sm. and *T. japonicus* (Petit) Temp. & H. Perag. have already been described in detail with both light and electron microscopy (Williams 1987, 1989). As a continuation of those studies, this paper describes a taxon Ehrenberg called *Bibliarium castellum* Ehrenb. (= *T. castellum* (Ehrenb.) Grunow) and a new fossil species from Inner Mongolia, *T. pseudocastellum*. I also offer some notes on other taxa possibly confused with *T. castellum*. While this study is limited to light microscopy only, it will serve as a focus for the further study of specimens under the scanning electron microscope if and when appropriate material is discovered and becomes available.

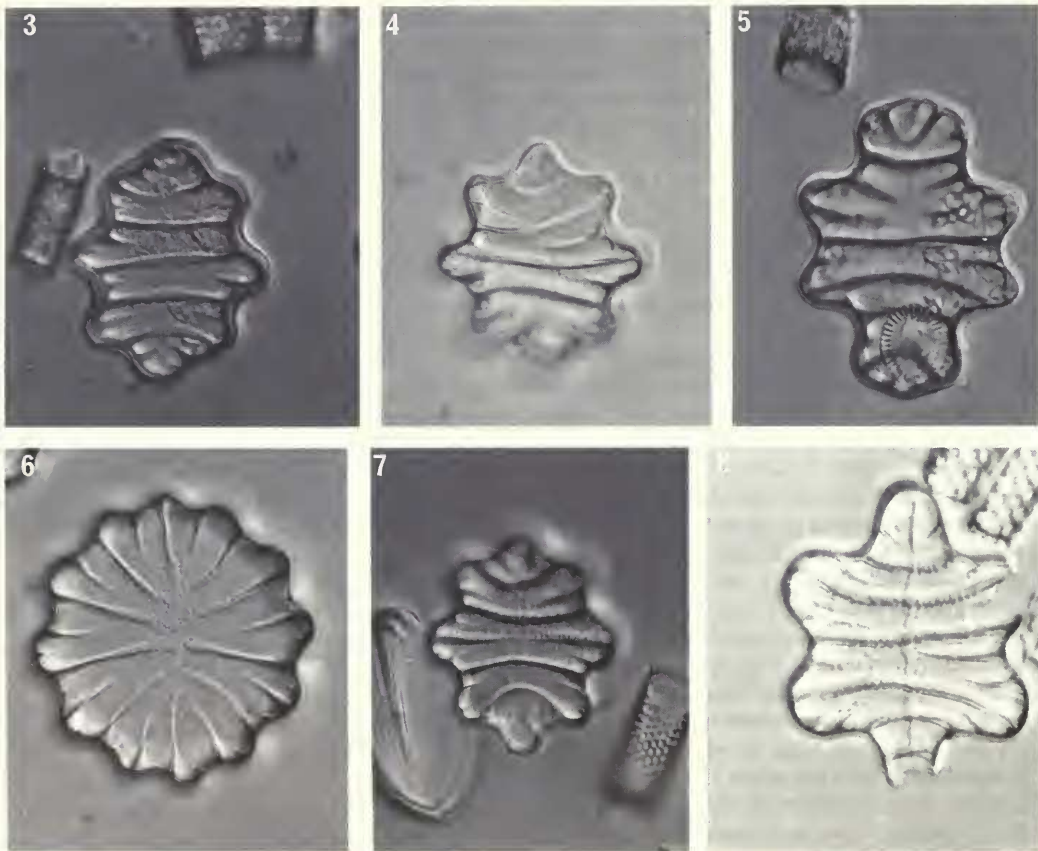
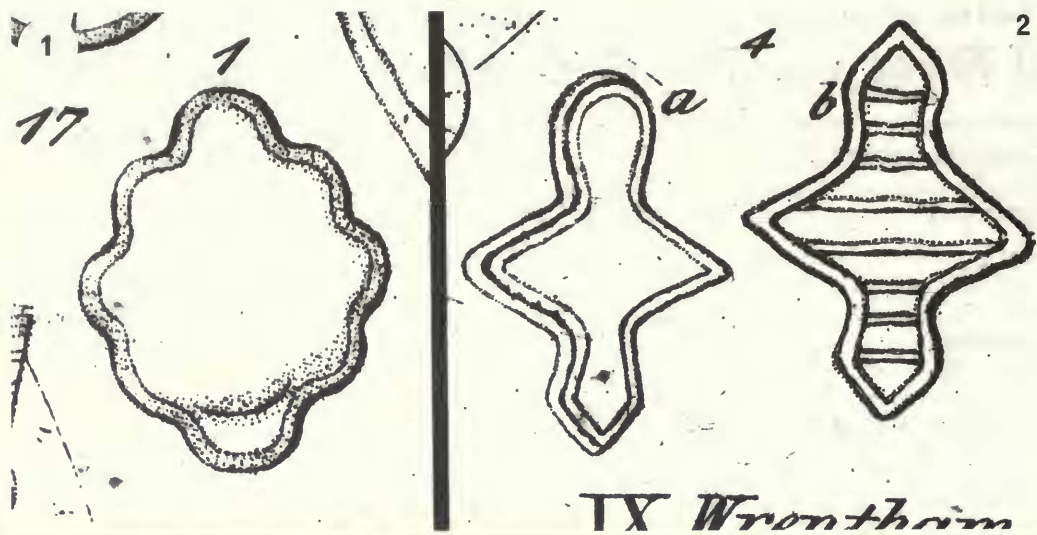
and its updated version Ross et al. (1979), are the standard references followed in this study. Stosch (1975) presented the first detailed discussion on girdle band morphology and nomenclature. However, since his pioneering effort much has been discovered and some of the conclusions reached in his paper are subject to debate and undoubtedly will be modified in due course; some aspects of possible modifications have been discussed by Mann (1982), Williams (1985), and Round et al. (1990). Additional commentary relevant to *Tetracyclus* morphology can also be found in Williams (1985, 1987, 1989, 1996).

SYSTEMATIC DESCRIPTIONS

***Tetracyclus castellum* (Ehrenb.) Grunow** in *Verh. zool.-bot. Ges. Wien* **12**: 411 (1862). – *Tetracyclus japonicus* sensu Lupikina in *Nov. Sist. Nizsh. Rast.* [1965]: pl. 3, figs 1-3 (1965); Khursevich & Loginova, *Iskopaemaya Diatomovaya Flora Belorussii (Sistematicheskii Obzor)*: pl. 17, fig. 13 (1980); Khursevich in *Acta geol. hung.* **28**: pl. II, fig. 7 (1982). – *Tetracyclus stellare* sensu J.Y. Li in *Bull. Inst. Geol. chin. Acad. geol. sci.* **5**: pl. 1, fig. 18 (1982); J.Y. Li & Y.Z. Qi in *Proc. 8th Internat. Diat. Symp.*: pl. 2, figs 4, 5 (1986); Valeva & Temniskova-Topalova in *Fitologiya* **46**: pl. III, figs 11, 12 (1993). – *Tetracyclus stellare* var. *exinia* sensu VanLand. in *Micropaleontology* **31**: pl. 1, fig. 9 (1985). – *Tetracyclus* sp. Tscheremisina, *Diatomovaya Flora Neogenovykh Otlozhenii Pribaikal'ya (Tunkinskaya Kotolovina)*: pl. 6, fig. 2 (1973).
Figs 1, 3, 4, 7.

TERMINOLOGY

A number of papers dealing with the particulars of diatom valve terminology have been published in the last 15 years. For the siliceous parts of the diatom valve and girdle, Anonymous (1975),



Figs 1, 3, 4, 7 *T. castellum*. Fig. 1: Reproduction of Ehrenberg (1854): pl. 33/2, fig. 1. Fig. 3: *Tetracyclus* '*costellatus*' from Temp. & Perag., *Diat. monde entier*, 2nd ed., slide no. 122, BM 68468, specimen 30 μ long. Fig. 4: *Tetracyclus elegans* var. *eximia* from Temp. & Perag., *Diat. monde entier*, 2nd ed., slide no. 122, BM 68468, specimen 25 μ long. Fig. 7: *T. 'costellatus'* var. *turris* from Temp. & Perag., *Diat. monde entier*, 2nd ed., slide no. 134, BM 68479, specimen 25 μ long.

Fig. 2 *Bibliarium elegans* reproduced from Ehrenberg (1854): pl. 33/2, fig. 4a, b.

Fig. 5 *T. emarginatus* var. *crassa* from Temp. & Perag., *Diat. monde entier*, 2nd ed., slide no. 122, BM 68468, specimen 40 μ long.

Fig. 6 *T. japonicus* from Temp. & Perag., *Diat. monde entier*, 1st ed., slide no. 79, BM 14331, specimen 55 μ long.

Fig. 8 *T. pseudocastellum*. Inner Mongolia, China, BM 81618, specimen 40 μ long.

Biblarium castellum Ehrenb. in *Ber. Akad. Wiss. Berlin* [1843]: 47 (1843), *nom. nud.* – Ehrenb. in *Ber. Akad. Wiss. Berlin* [1845]: 73 (1845). – Ehrenb. in *Mikrogeol.*: pl. 33/2, fig. 1 (1854). Type: ‘Ad Bargusinam Sibiriae fossile’, Ehrenberg (1843: 47), specimens not located. Iconotype = pl. 33/2, fig. 1 in Ehrenberg (1854).

?*Tetracyclus islandica* Østrup in *Meddr dansk geol. Foren.* 6: 28, pl. 1, fig. 1 (1900). Type: Illagil, Iceland (K 384-holotype?).

Tetracyclus costellatus Héríb., *Diat. foss. Auvergne*: 16, pl. 8, fig. 12 (1902), *orth. var.*, corrected to *castellum* in Perag. *Cat. Diat.*: 920 (1903). Type: ‘Dépot de Celles, Cantal’ (BM 68468-isotype).

Tetracyclus costellatus var. *turris* Perag. & Héríb. in Héríb. *Diat. foss. Auvergne*: 39, pl. 8, fig. 13 (1902), *orth. var.*, corrected to *castellum* in Perag., *Cat. Diat.*: 920 (1903). Type: ‘Dépot d’Auxillac, Cantal’ (BM 68479-3-isotypes).

Tetracyclus elegans var. *eximia* Héríb. & Perag. in Héríb., *Diat. foss. Auvergne*: 16, pl. 8, fig. 15 (1902). Type: ‘Dépot de Celles, Cantal’ (BM 68468-isotype).

Tetracyclus stellare Héríb., *Diat. foss. Auvergne*: 31, pl. 11, fig. 23 (1903). Type: ‘Dépot de Joursac, Cantal’ (BM 68397–99-isotypes).

Tetracyclus stellare var. *eximia* (Héríb.) Hust. in *Abh. naturw. Ver. Bremen* 23: 98 (1914).

Tetracyclus lapponicus Tynni in *Bull. geol. Surv. Finl.* 320: 35, pl. 19, figs 10–15 (1982). Type: ‘Gyttya deposit of Sivakkapalo’ (GTL HH/80-holotype, not seen).

Tetracyclus chudjakovii Pushkar in *Paleobot. Fitostrat. Vostoka SSSR*: 114, pl. 22, figs 15–17 (1983) (AH CCCP 123/30-79-Û-holotype, not seen).

Valves with 8 equally spaced points somewhat resembling a ‘star’, 25–45 µ (n=10) in diameter, each tip curving at its margin (Li & Qi, 1986: pl. 2, fig. 4). Transapical ribs primary (25–45 in 10 µ), radiate; secondary and tertiary ribs present, extending into each point of the star and meeting at the sternum; striae in equidistant rows. Cingulum consisting of open septate bands. Septum small, not visible in a number of bands (= secondary copulae?) (Fig. 1, septum visible in Ehrenberg’s illustration; Li & Qi, 1986: pl. 2, fig. 5).

Material examined

Living

Iceland. ‘Illagil. Tinnárdalur, Skagafhordssýssel . . .’ (K 384, holotype? of *Tetracyclus islandica*).

Fossil

France. Cantal, Joursac, BM 68397-99 (Isotypes of *Tetracyclus stellare*, Temp. & Perag., *Diat. monde entier*, 2nd ed., nos 51–53); Cantal, Celles, BM 68468 (Isotype of *Tetracyclus costellatus*, *T. elegans* var. *eximia*, and *T. emarginatus* var. *crassa*, Temp. & Perag., *Diat. monde entier*, 2nd ed., no. 122); Cantal, Auxillac, BM 68479-3 (Isotype of *T. costellatus* var. *turris*, Temp. & Perag., *Diat. monde entier*, 2nd ed., nos 133–137).

U.S.A. Nevada, Esmeralda Co., SW of Loric Mountain and west of Tonopato Esmeralda formation, USGS 5078 (CAS 382005).

What is understood as *Tetracyclus castellum* is based upon type material from synonymous taxa, as Ehrenberg’s material is unavailable. In addition five valves were discovered in a fossil deposit from the U.S.A. (Tonopato Esmeralda formation, CAS 382005). As the species is known from so few specimens the synonymy requires further comment.

Biblarium castellum – Ehrenberg (1843) described the species *Biblarium castellum* from a fossil deposit in Siberia (‘Infusorien-

Lager von Bargusina im Gouvernement Irkutsk in Sibirien’, Ehrenberg, 1843: 46; ‘Ad Bargusinam Sibiriae fossile’, Ehrenberg, 1845: 73). Although Ehrenberg provided a reasonable (for his time) description (‘B. corpusculorum valvis (intermediis) ovatis obtusis, sinibus marginalibus utrinque quatuor. Laterales valvae nondum observatae’, Ehrenberg, 1845: 73), he offered only one illustration in the *Mikrogeologie* (Ehrenberg, 1854: pl. 33/2, fig. 1, reproduced here as Fig. 1). The specimen he chose to illustrate is clearly of a girdle band and provides no information on valve structure, of which Ehrenberg appeared to have no knowledge (‘Laterales valvae nondum observatae.’ Ehrenberg, 1845: 73). Ralfs (in Pritchard, 1861: 806) added nothing of significance to the species description, reproducing Ehrenberg’s figure (in Pritchard, 1861: pl. iv, fig. 44) and translating his 1845 text (‘Lateral view of central portion elliptic, with obtuse ends, and four marginal undulations . . . Lateral valves unknown’, Pritchard, 1861: 806). Although Grunow (1862: 411) transferred the species to the genus *Tetracyclus*, he also appears not to have investigated relevant material and again relied only on Ehrenberg’s description and figure. This approach continued with De Toni referring to Ehrenberg, Grunow, and Ralfs (all of whom used the same single specimen) for his own description of this species for which he was able to provide additional perspective: ‘Valvis late ovatis, obtusis, subrhomboideis, marginibus triundulatus...’ (De Toni, 1892: 748). In summary, *Tetracyclus castellum* has remained a valid name based on Ehrenberg’s one girdle band specimen for which type material has been unavailable for examination, one imagines, since Ehrenberg’s time. However, it is possible to suggest two things from this illustration of a girdle specimen: first, that the valves would be similar in shape, that is like an 8-pointed star; and second, that the girdle has a septum (Fig. 1).

Tetracyclus ‘costellatus’ – When Héribaud undertook his study of the fossil diatoms of Auvergne in France he made the new combination *Tetracyclus costellatus* based on *Biblarium costellatum*, attributing the specific epithet to Ehrenberg (Fig. 3; Héribaud, 1902: 16, pl. 8, fig. 12). In the same volume, Tempère & Héribaud described the new variety *T. costellatus* var. *turris* (Fig. 7; Héribaud, 1902: 39, pl. 8, fig. 15), again with reference to the *Biblarium costellatum* of Ehrenberg (Lauby [1910: 340], in a study of the same area, also used the name *T. costellatum*). Ehrenberg never used the name *costellatum* in connection with the genus *Biblarium*. That Héribaud made an error with the name was identified by Peragallo (1903: 920) who corrected both names. Mills (1935: 1600) included *Tetracyclus costellatus* (and the variety *turris*) in his catalogue as a synonym of *T. castellum* (to compound confusion Mills misspelt *T. costellatus* as *T. constellatus*). VanLandingham acknowledged that Héribaud’s usage of the name *T. costellatus* was a misspelling of *castellum* (‘error? for *Biblarium castellum* Ehrenberg 1843...’, VanLandingham, 1978: 3981) and included it as an orthographic variant of *T. castellum*.

Isotype material for *T. ‘costellatus’* and *T. ‘costellatus’* var. *turris* are available as part of Tempère & Peragallo’s *Diatomées du monde entier* exiccata set (2nd ed., slide no. 122, BM 68468; slide nos 133–137, BM 68479-83) and although rare, a few specimens have been examined (Figs 3, 7). In each case the valves are 8-pointed stars suggesting that they can be usefully compared with Ehrenberg’s *Biblarium castellum*.

Tetracyclus elegans*, *T. elegans* var. *eximina*, *T. emarginatus* var. *crassa*, and *T. stellare – *Tetracyclus elegans* (Ehrenb.) Héríb. was based upon another Ehrenberg species, *Biblarium elegans*, described from the same Siberian fossil deposit as *B. castellum* (Ehrenberg, 1854: 90, pl. 33/2, fig. 4a, b). Ehrenberg provided no description and only published illustrations of two specimens, one

valve and one girdle band (Ehrenberg, 1854, pl. 33/2, fig. 4a, b; reproduced here as Fig. 2). Ralfs transferred the species to *Tetracyclus*, providing a minimal description ('Inflations acute') and noting that 'Ehrenberg's figure of this species differs from *T. rhombus* merely in its more developed inflation' (Ralfs in Pritchard, 1861: 806–7). De Toni, however, differed from Ralfs and in his view likened *T. elegans* to *T. lacustris* Ralfs (= *T. glans* (Ehrenb.) Mills; see Williams, 1987). *T. rhombus* (Ehrenb.) Ralfs in Pritchard has been discussed in more detail in Williams (1996) and *T. glans* in Williams (1987). Briefly, Ehrenberg's original illustrations of *T. rhombus* included drawings of specimens from Siberia and a U.S.A. fossil deposit from Columbia River (Ehrenberg, 1854: pl. 33/12, figs 7, 8, pl. 33/2, figs 9, 9*, 10; see Williams, 1996, for notes on the Columbia River deposit). From the illustrations alone, it appears that specimens from Siberia (Ehrenberg, 1854: pl. 33/2, figs 9, 9*, 10) may indeed belong to *T. glans* (or some closely related species, e.g. *T. pagesi* Hér. or *T. stella* (Ehrenb.) Hér.; cf. Hustedt, 1914: 101, 105; Williams, in prep.) while the Columbia River specimens (Ehrenberg, 1854: pl. 33/12, figs 7, 8) are probably a small pre-auxospore stage of some elliptical-valved species (see Williams, 1990, 1996). Until Siberian material has been examined these conclusions must be considered unsubstantiated. However, it does explain Ralfs' and De Toni's conflicting views noted above.

Hér. & Peragallo unnecessarily transferred *Biblarium elegans* to *Tetracyclus* (Hér. & Perag., 1902: 16; Ralfs had already done so). However, part of their reason was to be able to describe further specimens they encountered in the 'Celles' deposit as *Tetracyclus elegans* var. *eximia* (Hér. & Perag., 1902: 16, pl. 8, fig. 15). Isotype material is available (Temp. & Perag., *Diat. monde entier* 2nd ed., slide no. 122, BM 68468) and, although only a few specimens were encountered, they are 8-pointed star-shaped valves like *T. castellum* (Fig. 4).

In a later volume of the same study, Hér. & Peragallo published another new species under the name of *Tetracyclus stellare* Hér. from the Joursac deposit of Cantal (Fig. 7; Hér. & Perag., 1903: 31, pl. 11, fig. 23). According to Hér. & Peragallo *T. stellare* is '... intermédiaire entre le *Tetracyclus castellum* et le *Tetracyclus elegans*, dont il nous paraît une forme dérivée' (Hér. & Peragallo 1903: 31). This is clearly referring to the shape of the valve outline. Hustedt concluded that *Tetracyclus elegans* var. *eximia* was perhaps better understood as a variety of *T. stellare* and that *T. elegans* was better understood as a variety of *T. lacustris* (= *T. glans*) and transferred both taxa accordingly (Hustedt, 1914, p. 97 for *elegans*, p. 98 for *stellare*; unfortunately, Hustedt refers to *stellare* as *stellaris* throughout his monograph). There is merit in Hustedt's decisions but once again, the absence of Ehrenberg's Siberian material makes judgment difficult. Nevertheless, inspection of specimens of *T. stellare* (as well as *T. elegans* var. *eximia*) indicates that there is as yet insufficient evidence to relate it most closely to either *T. elegans* or *T. glans* and is best considered as a synonym of *T. castellum*.

Finally, Hér. & Peragallo described a new variety of *Tetracyclus emarginatus*, *T. emarginatus* var. *crassa* Hér. & Perag. (Hér. & Peragallo, 1902: 16, pl. 8, fig. 16; specimens from Temp. & Perag., *Diat. monde entier* 2nd ed., no. 122, BM 68468; Fig. 5). This taxon only superficially resembles *T. castellum* and should perhaps be considered in the context of *T. emarginatus* to which it appears more similar.

Tetracyclus islandica, *T. lapponicus*, and *T. chudjakovii* – Østrup described the new species *Tetracyclus islandica* from Illagil in Iceland (Østrup, 1900: 28, pl. 1, fig. 1). He made no attempt at a description but drew attention to the unusual shape which he felt

made its unique status obvious ('... som uden at kraeve naermere Beskrivelse, tydeligt fremgaar af Tab. nost. Fig. 1', Østrup, 1900: 28). There is only one relevant slide of type material present in C of which J.B. Hansen wrote: 'Østrup used to keep raw and cleaned material of everything but in a few cases where the material is scanty there are only slides available. You have got the only material I can find' (Hansen, pers. comm.). The specimens on this slide were rather rare and too poor to make useful micrographs. However, it was clear that the 'edges' of the valve were somewhat more rounded than in Østrup's published illustration, suggesting that it too should be considered a synonym of *T. castellum*. This is an interesting conclusion as it implies that *T. castellum* should properly be considered as a sixth (albeit rare) living species of *Tetracyclus*. Further material needs to be examined, especially using electron microscopy.

Tetracyclus lapponicus Tynni was described as a Neogene fossil from the 'Gyttya deposit in Finland' (Tynni, 1982: 35, pl. 19, figs 7, 10–15). Tynni suggested that it 'closely resembles the form *T. japonicus* described from the Neogene stratum of White Russia (Khursevich & Loginova 1980)'. Khursevich & Loginova's (1980) specimen is one of *T. castellum* (see below) and hence *T. lapponicus* should also be considered a synonym of *T. castellum*. Tynni remarks that '*T. ellipticus* var. *lancea* f. *subrostrata* Hust. – *T. lapponicus* with their intermediate forms constitute a transitional series... from which it becomes evident that *T. ellipticus* and *lapponicus* are closely related forms.' (Tynni, 1982: 35). Material has not been examined but evidence presented by Tynni (1982: pl. 19, figs 7, 10–15) does not seem to support his contention and he relies on an unconventional understanding of *T. ellipticus* var. *lancea* f. *subrostrata* (see Williams, 1996).

Finally, Pushkar described the new species *Tetracyclus chudjakovii* Pushkar (1983: 114, pl. 22, figs 15–17) also with an 8-pointed star-shaped valve and again probably a specimen of *T. castellum*.

SUMMARY. Specimens which appear to be *T. castellum* (not forgetting that this taxon was originally based on one illustration of a girdle band) have been described on a number of different occasions after Ehrenberg, from 1903 to 1983, including *T. 'castellatus'*, *T. elegans* var. *eximia*, *T. stellare*, *T. islandica*, *T. lapponicus*, and *T. chudjakovii*. No doubt much of this re-description is due to poor knowledge of genuine *T. castellum* specimens. To compound matters other errors have crept in, possibly due to peculiarities surrounding its nomenclature, especially an early confusion involving several different usages of the name *Tetracyclus japonicus*, clearly a different species from *T. castellum* as it has a valve like a 12-pointed star (Fig. 6, *T. japonicus* sensu stricto; see also Williams, 1989).

Other illustrations with different names include Lupikina (1965: pl. 3, figs 1–3) and Khursevich & Loginova (1980: pl. 17, fig. 13; see also Khursevich, 1982: pl. II, fig. 7; both illustrations are of the same specimen, the latter being turned upside down) who named specimens of this taxon *T. japonicus*; Li (1982b: pl. 1, fig. 18) and Valeva & Temniskova-Topalova (1993: pl. III: figs 11, 12) who named specimens *T. stellare*; VanLandingham (1985: pl. 1, fig. 9) who named specimens *T. stellare* var. *eximia*; and Tscheremisina (1973: pl. 6, fig. 2) who named specimens *Tetracyclus* sp. All these illustrations seem to be of the same taxon and should be considered representatives of *T. castellum*. More recently additional specimens have been encountered from Kamchatka (Ozornina, 1993 and pers. comm.).

One notable exception is the specimens illustrated by Li (1982a) and Li & Qi (1986) which they erroneously called *T. peragalli* Hér. (see Williams, 1990). Examination of relevant material from their Chinese deposit reveals specimens that more correctly belong to a new species, a description of which is given below.

Tetracyclus pseudocastellum D.M. Williams, sp. nov.
Fig. 8.

Tetracyclus peragalli sensu J.Y. Li & Y.Z. Qi in *Proc. 8th Internat. Diat. Symp.*: pl. 2, figs 3, 6 (1986).

Valves with 6 equally spaced points somewhat resembling a 'star', each point rounded at the margin, 20–45 μ (n=7) in diameter. Striae in equidistant rows; ribs predominantly primary, with few secondary ribs extending between the points of the star. Cingulum consisting of open septate bands (Li & Qi, 1986: pl. 2, figs 3, 6). Septum small, difficult to observe in a number of bands (those are possibly secondary copulae). Known only from type material.

TYPE. Late Miocene flora of Inner Mongolia, China. BM 81618, 'No: SZ₁₁-1 (9) IM, China', specimen marked number 5-holotype; IGC-Beijing SZ₁₁-1-01 IMS-isotype.

Material examined

China. *Miocene*, Den Hua Jiling Province and Shangdu County of Inner Mongolia, BM 81618, 'No: SZ₁₁-1 (9) IM, China'.

T. pseudocastellum is known only from the type locality and is easily distinguished by the number of points of the valve: 6 for *pseudocastellum* (Fig. 8), 8 for *castellum* (Figs 3, 4, 7), and 12 for *japonicus* (Fig. 6). Only the latter species is known from a detailed study of its morphology (Williams, 1989). Detailed comparison of valve and girdle structure of these species will allow them to be placed in relation to each other as well as other species of *Tetracyclus*. The (palaeo)biogeographical interpretation of the genus is largely around the Pacific rim, an understanding of the relationships of the species will allow a better understanding of the causes of this distribution (Williams 1996).

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REFERENCES

- Anonymous.** 1975. Proposals for a standardization of diatom terminology and diagnoses. *Beih. nov. Hedwigia* **53**: 323–354.
- De Toni, G.B.** 1892. *Sylloge Algarum* **2**(2). Patavii.
- Ehrenberg, G.C.** 1843. Mittheilungen über 2 neue asiatische Lager fossiler Infusorien-Erden aus dem russischen Trans-Kaukasien (Grusien) und Siberien. *Ber. Akad. Wiss. Berlin* [1843]: 43–49.
- 1845. Neue Untersuchungen über das kleinste Leben als geologisches Moment. *Ber. Akad. Wiss. Berlin* [1845]: 53–88.
- 1854. *Mikrogeologie*. Leipzig.
- Grunow, A.** 1862. Die österreichischen Diatomeen nebst Anschluss einiger neuen Arten von andern Lokalitäten und einer kritischen Übersicht der bisher bekannten Gattungen und Arten. Erste Folge. Epithemieae, Meridioneae, Diatomeae, Entopyleae, Surirellae, Amphipleureae. *Verh. zool.-bot. Ges. Wien* **12**: 315–472.
- Héribaud, J.** 1902. *Les Diatomées fossiles d'Auvergne*. 1st Memorie. Paris.
- 1903. *Les Diatomées fossiles d'Auvergne*. 2nd Memorie. Paris.
- Hustedt, F.** 1914. Die Bacillariaceen-Gattung *Tetracyclus* Ralfs; kritische Studien über Bau und Systematik der bisher beschriebenen Formen. *Abh. naturw. Ver. Bremen* **23**: 90–107.
- Khursevich, G.K.** 1982. Neogene diatom assemblages from Byelorussia and their stratigraphic significance. *Acta geol. hung.* **28**: 123–134.
- & **Loginova, L.P.** 1980. *Iskopaemaya Diatomovaya Flora Belorussii* (*Sistematicheskii Obzor*). Minsk.
- Lauby, A.** 1910. Recherches paléophytologiques dans le Massif central. *Bull. Serv. Carte géol. détaill. France* **20**: 1–398.
- Li, JiaYing** 1982a. Miocene diatom assemblages of Shanwang, Shandong Sheng. *Acta bot. sin.* **24**: 456–467.
- 1982b. Genus *Tetracyclus* and its stratigraphic significance. *Bull. Inst. Geol. chin. Acad. geol. sci.* **5**: 149–166.
- 1984. Some new species and varieties of the genus *Tetracyclus* Ralfs (Bacillariophyta). *Acta phytotax. sin.* **22**: 231–236.
- & **Qi Yu Zao** 1986. Neogene diatom assemblages in China. In M. Ricard (Ed.), *Proc. 8th Internat. Diat. Symp.*: 699–711.
- Lupikina, E.G.** 1965. Diatomeae novae et curiosae e stratis Ermanicis partis Kamczatkae occidentalis. *Nov. Sist. Nizsh. Rast.* **1965**: 15–22.
- Mann, D.G.** 1982. Structure, life history and systematics of *Rhoicosphenia* (Bacillariophyta). I. The vegetative cell of *Rh. curvata*. *J. Phycol.* **18**: 162–176.
- Mills, F.W.** 1935. *An index to the genera and species of the Diatomaceae and their synonyms, 1816–1932*. **21**: 1571–1726. London.
- Østrup, E.** 1900. Diatomerne i nogle islandiske. Surtarbrand-Lag. II. *Meddr dansk geol. Foren.* **6**: 23–30.
- Ozornina, S.** 1993. *Diatoms and problems of stratigraphy of the Eopleistocene and the late Pleistocene of Central Kamchatka*. Doctoral Thesis, Vladivostock.
- Peragallo, M.** 1903. *Le catalogue général des Diatomées*. **2**: 472–973. Clermont-Ferrand.
- Pritchard, A.** 1861. *A history of infusoria including the Desmidiaceae and Diatomaceae, British and foreign*. 4th ed. London.
- Pushkar, V.S.** 1983. Novyi vid roda *Tetracyclus* Rales [sic] (Bacillariophyta) ie miotsena severnogo skhotena alinya In V.A. Krasilov (Ed.), *Paleobotanika i Fitostratigrafiya Vostoka SSSR*: 112–115.
- Ross, R., Cox, E.J., Karayeva, N.L., Mann, D.G., Paddock, T.B.B., Simonsen, R. & Sims, P.A.** 1979. An amended terminology for the siliceous components of the diatom cell. *Beih. nov. Hedwigia* **64**: 513–533.
- Round, F.E., Crawford, R.M. & Mann, D.G.** 1990. *The diatoms*. Cambridge.
- Stosch, H. A. von.** 1975. An amended terminology of the diatom girdle. *Beih. nov. Hedwigia* **53**: 1–35.
- Tempère, J. & Peragallo, H.** 1907–1915. *Les Diatomées du monde entier. Collection Tempère et Peragallo* (2e édition). Arcachon. [See note in R. Ross 1995 *Bull. Br. Mus. nat. Hist. (Bot.)* **25**: 93 concerning the citation of this work.]
- Tscheremisnina, E.A.** 1973. *Diatomovaya Flora Neogenovykh Otlozhenii Pribaikal'ya* (*Tunkinskaya Kotlovina*). Novosibirsk.
- Tynni, R.** 1982. The reflection of geological evolution in tertiary and interglacial diatoms and silicoflagellates in Finnish Lapland. *Bull. geol. Surv. Finl.* **320**: 1–40.
- Valeva, M.T. & Temniskova-Topalova, D.M.** 1993. Diatom analysis of Neogene sediments from the Karlov coal basin I. *Fitologiya* **46**: 67–84.
- Van Landingham, S.L.** 1978. *Catalogue of the fossil and recent genera and species of diatoms and their synonyms*. **7**. Vaduz.
- 1985. Potential Neogene diagnostic diatoms from the Western Snake River Basin, Idaho and Oregon. *Micropaleontology* **31**: 167–174.
- Williams, D.M.** 1985. Morphology, taxonomy and interrelationships of the ribbed araphid diatoms from the genera *Diatoma* and *Meridion* (Diatomaceae: Bacillariophyta). *Bibl. Diat.* **8**: 1–228.
- 1987. Observations on the genus *Tetracyclus* Ralfs (Bacillariophyta) I. Valve and girdle structure of the extant species. *Br. phycol. J.* **22**: 383–399.
- 1989. Observations on the genus *Tetracyclus* Ralfs (Bacillariophyta) II. Morphology and taxonomy of some species from the genus *Stylobilium*. *Br. phycol. J.* **24**: 317–327.
- 1990. Examination of auxospore valves in *Tetracyclus* from fossil specimens and the establishment of their identity. *Diatom Res.* **5**: 189–194.
- 1996. Fossil species of the diatom genus *Tetracyclus* (Bacillariophyta, 'ellipticus' group): Morphology, interrelationships and the relevance of morphogenesis to phylogeny. *Phil. Trans. R. Soc. Ser. B.* **351**: 1759–1782.